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WOOD ANATOMY OF GNETALES IN A FUNCTIONAL, ECOLOGICAL, AND EVOLUTIONARY CONTEXT

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ABSTRACT

New scanning electron microscope (SEM) and light microscope data and illustrations are presented in order to compare hydraulic adaptations of non-gnetalean conifers and angiosperms to relevant wood features of Gnetales. Gnetales have essentially all of the adaptations of both groups, yet have not competed well, despite predating angiosperms in origin and radiation. Angiosperms may be advantaged more by life cycle abbreviation and by heterochronic possibilities than by wood features. Wood features of Gnetales that relate to conduction (torus-margo differentiation of tracheid pit membranes, distribution of tori within the wood, perforation plate simplification, growth rings, vesturing, helical thickenings, and axial parenchyma) are reviewed in the light of recent work that demonstrates the physiological significance of these features in angiosperms. The various xylary adaptations of *Ephedra*, *Gnetum*, and *Welwitschia* are analyzed in terms of conductive efficiency versus conductive safety, and in turn, compared to the habitats of the three genera, respectively: *Ephedra* and *Welwitschia* survive in rather extreme habitats, whereas *Gnetum* competes in mesic forest by what may be minor shifts among basically similar niches. Gnetales have essentially all of the wood anatomical advantages of angiosperms, except for ability to shift degrees of wood anatomical juvenilism or adulthood—an important angiosperm advantage. The relatively lengthy life cycle of Gnetales, requiring female gametophyte formation prior to embryo formation (vs. simultaneous endosperm and embryo development in angiosperms) and the related requirement for at least several years' growth prior to seed formation are probably the prime reasons for lack of gnetalean success. Wood features should be interpreted as adapted to the present-day ecology of a woody species, and ideas that evolutionary flexibility to shift into more seasonal conditions is hindered by rigid wood formulas (which actually can change rather rapidly) should be questioned. Wood evolution of Gnetales, like that of angiosperms, can be regarded as a series of shifts in the trade-offs between conductive efficiency and conductive safety.

Key words: conductive safety, coniferous wood, ecological wood anatomy, lianas, successive cambia.

INTRODUCTION

Wood of Gnetales has now been studied in detail with respect to comparative anatomy (Carlquist 1988, 1989, 1992, 1994, 1996*a*,*b*,*c*; Carlquist and Gowans 1995; Carlquist and Robinson 1995). These studies, along with those in other fields, laid the groundwork for confirmation of the concept (Thompson 1918) that Gnetales are coniferalean (''gnetifers,'' ''gnepines'': Burleigh and Mathews 2004) in their relationships. Molecular data (Bowe et al. 2000; Donoghue and Doyle 2000) demonstrated the unlikelihood of the ''anthophyte'' hypothesis that for much of the 20th century favored Gnetales as the group closest to angiosperms.

Gnetalean wood does have vessels, albeit different from those of angiosperms. The presence of vessels was alleged by some workers to indicate relationship between angiosperms and Gnetales. The very real differences between gnetalean vessels and angiosperm vessels were not noted, with the tacit assumption that there was only one kind of vessel, one origin of vessels. Other wood features were also claimed to indicate relationship. The similarities proved to be homoplasies. These convergences, however, do open another line of analysis: in what ways are wood features functionally like those of angiosperms, in which respects are they like those of non-gnetalean conifers? In order to understand the relevant anatomical features, new studies, both with SEM (Fig. 1–24) and with light microscopy (Fig. 25–37), have been undertaken here. The features reported here are only those that are concerned, directly or indirectly, with hydraulic processes in gnetalean woods.

A surprising amount of relevant new work is also now available in the fields of wood physiology, ecology, paleobotany, and molecular phylogeny. Such new information led to a reassessment of the relationship between structure and function in angiosperm woods (Carlquist 2012). Recent work in wood physiology, cited herein, has established the functional value of wood histological features, so that such a reassessment is not really speculative, but merely applies principles that have been demonstrated.

Extant Gnetales consist of approximately 50 species of *Ephedra* L., 40 of *Gnetum* L., and one of *Welwitschia* Hook.f. (Price 1996). The vegetative distinctions between these genera are familiar to most botanists. Gnetales have a relatively long fossil history; the three genera were already distinct in the lower Cretaceous (Dilcher et al. 2005; Rydin et al. 2006; Yang 2010). Gnetalean (ribbed) pollen grains have been found in sediments as old as the Triassic, but probable macrofossils also date from Permian times (Crane 1996; Wang 2004). Thus, Gnetales probably predated angiosperms and have coexisted with them since lower Cretaceous time. *Gnetum* apparently has a more recent origin, in the Eocene (Won and Renner 2006).

An issue of central importance here is what role conductive capabilities have played in the relative success of Gnetales and of angiosperms. If Gnetales have essentially all of the conductive features of angiosperms (admittedly acquired independently) and essentially all of the features of non-gnetalean conifers, do any of these characters play a role in the relative success of Gnetales, non-gnetalean conifers, and angiosperms, respectively, or do we need to look elsewhere to

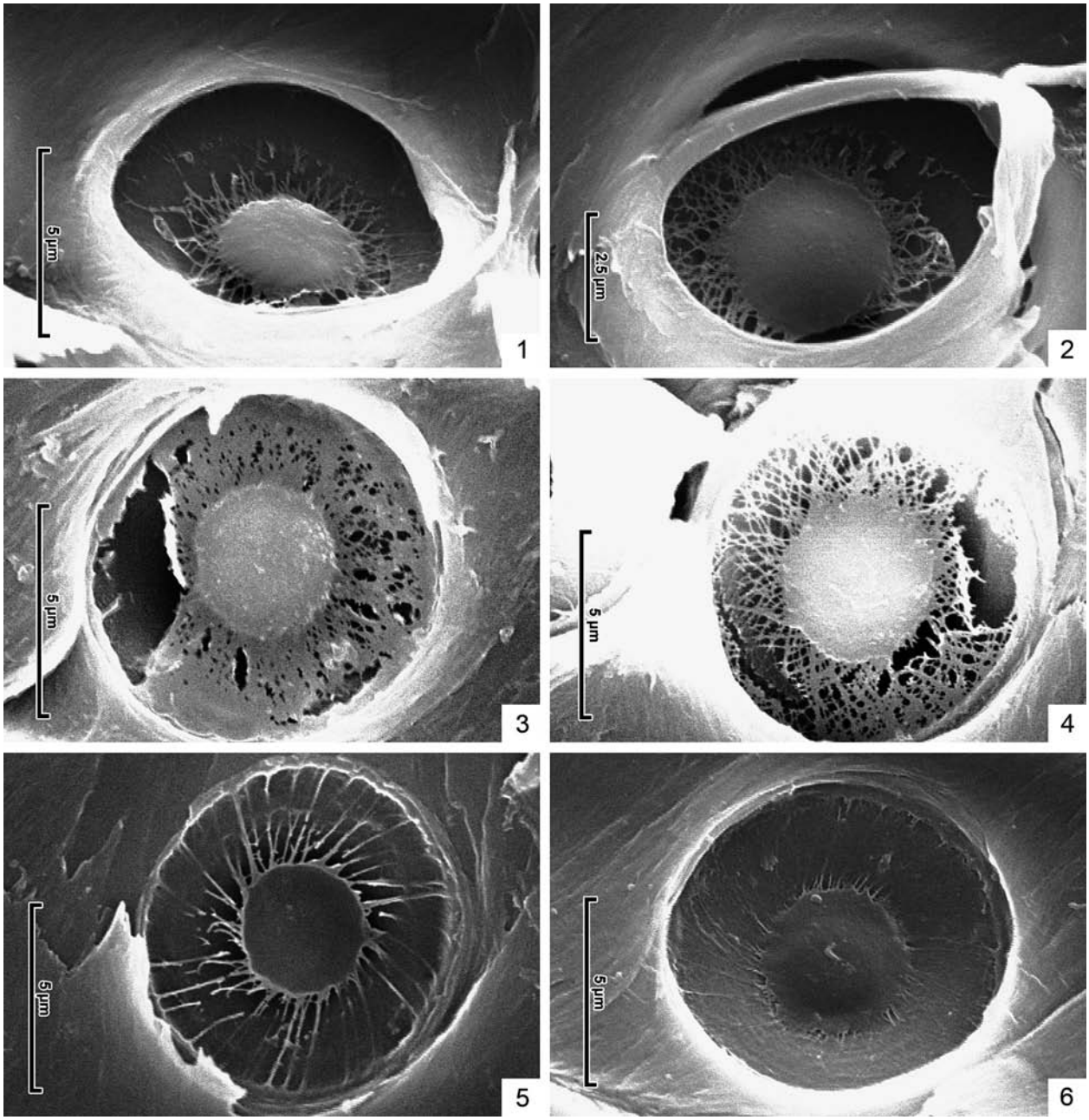

Fig. 1–6. SEM micrographs of pit membranes of tracheid pits from tangential sections of wood of *Ephedra nevadensis*.—1. Pit with margo threads partly adherent to the pit border.—2. Pit with threadlike margo threads, only some of which (at right) are adherent to the pit border.—3. Pit membrane free from pit border; pores are rather small.—4. Non-aspirated pit membrane; meshwork-like pattern of margo threads is visible.—5. Pit membrane that is displaced by aspiration, with many of the margo threads adherent to the pit border, but major ones still clearly visible.—6. Fully displaced pit membrane, with margo threads adherent to the pit border.

explain the differential success and distribution of the three groups? Recent analyses of angiosperms (Carlquist 2009, 2012) provide templates that we can apply to Gnetales.

MATERIALS AND METHODS

The species studied and the herbarium specimens documenting them are as follows: *Ephedra fasciculata* A.Nelson (between Kelso and Baker, San Bernardino County, California, *Carlquist 15862*, RSA); *E. nevadensis* S.Watson (cultivated at Santa Barbara Botanic Garden, SBBG); *E. pedunculata* Engelm. ex S.Watson, (near Del Rio, Texas, *Carlquist 15815*, RSA); *E. trifurca* Torr. (Yuma sand dunes, Arizona, MADw-11270); *Gnetum africanum* Welw. (Cameroon, *Fay 9000*, K); *G. cuspidatum* Blume (Bukit Anas, Kuala Lumpur, Malaysia, *Carlquist 8091*, RSA); *G. gnemon* L. (University of Malaysia campus, Kuala Lumpur, *Carlquist 8088*, RSA); hypocotyl of *Welwitschia mirabilis* Hook.f., (Swakopmund, Namibia, *Carlquist 8071*, RSA).

All materials were preserved in 50% aqueous ethanol except for the xylarium specimen from Forest Products Laboratory, Madison (*Ephedra trifurca*), which was a dried specimen. That

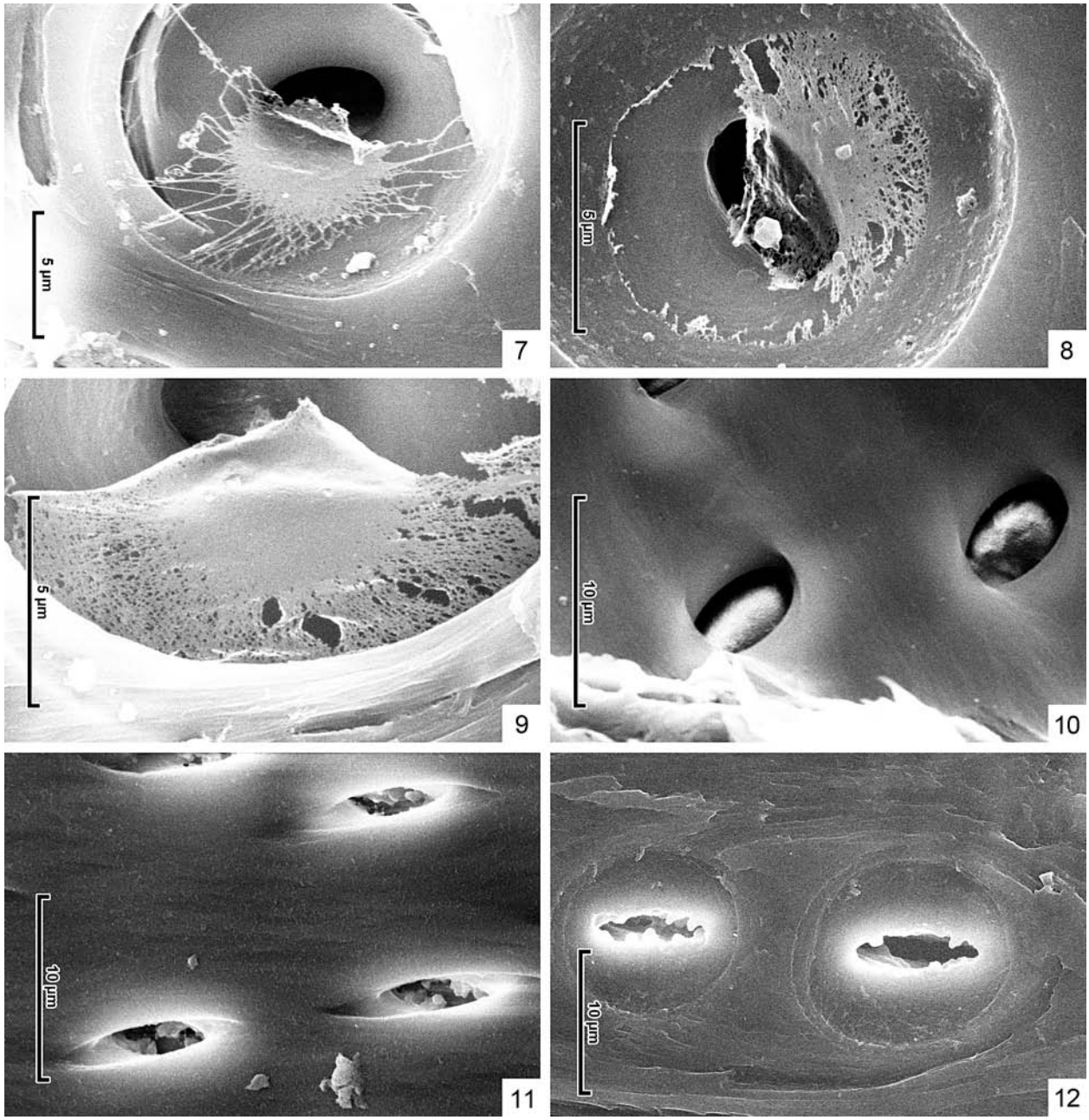

Fig. 7–12. SEM micrographs of tracheary elements of tangential sections of wood of *Gnetum.* 7–10, 12. *Gnetum cuspidatum.*—7–9. Pit membranes from sectioned pits of tracheids.—7. Pit membrane (upper half torn) with slender margo threads.—8. Pit membrane portion with meshwork-like margo, outer part of margo attached to pit border because of pit membrane displacement.—9. Portion of pit membrane with porous margo (several tears in margo evident).—10–11. Views of inner surfaces of tracheary elements.—10. Tracheid, with margos visible through the pit apertures.—11. *Gnetum africanum*. Vestured pits of vessel.—12. *Gnetum cuspidatum*. Vestured pits of vessel, seen from outer surface of vessel.

specimen was boiled, stored in 50% ethanol, and sectioned on a sliding microtome. Sections for study with light microscopy were softened with ethylene diamine, embedded in paraffin, sectioned according to the procedures of Carlquist (1982), and stained with a safranin-fast green combination. For studies with SEM, unsoftened material was sectioned either with a sliding microtome or with single-edged razor blades. Sections were dried between pairs of glass slides with pressure applied to assure flatness, sputter-coated with gold, and examined with a 2600N Hitachi scanning electron microscope.

RESULTS

Torus-Margo Nature of Tracheid Pit Membranes

Ephedra.—The bordered pits in *Ephedra* were shown earlier to have pit membranes that show torus-margo differentiation (Carlquist 1992). New SEM studies of *E. nevadensis* (Fig. 1–6) show that appearances can vary within a single section. In Fig. 2, we see threadlike margo strands, forming an open mesh, sometimes reticulate. In Fig. 3, the margo is composed of a porous lamina rather than threads. Figure 4 shows an

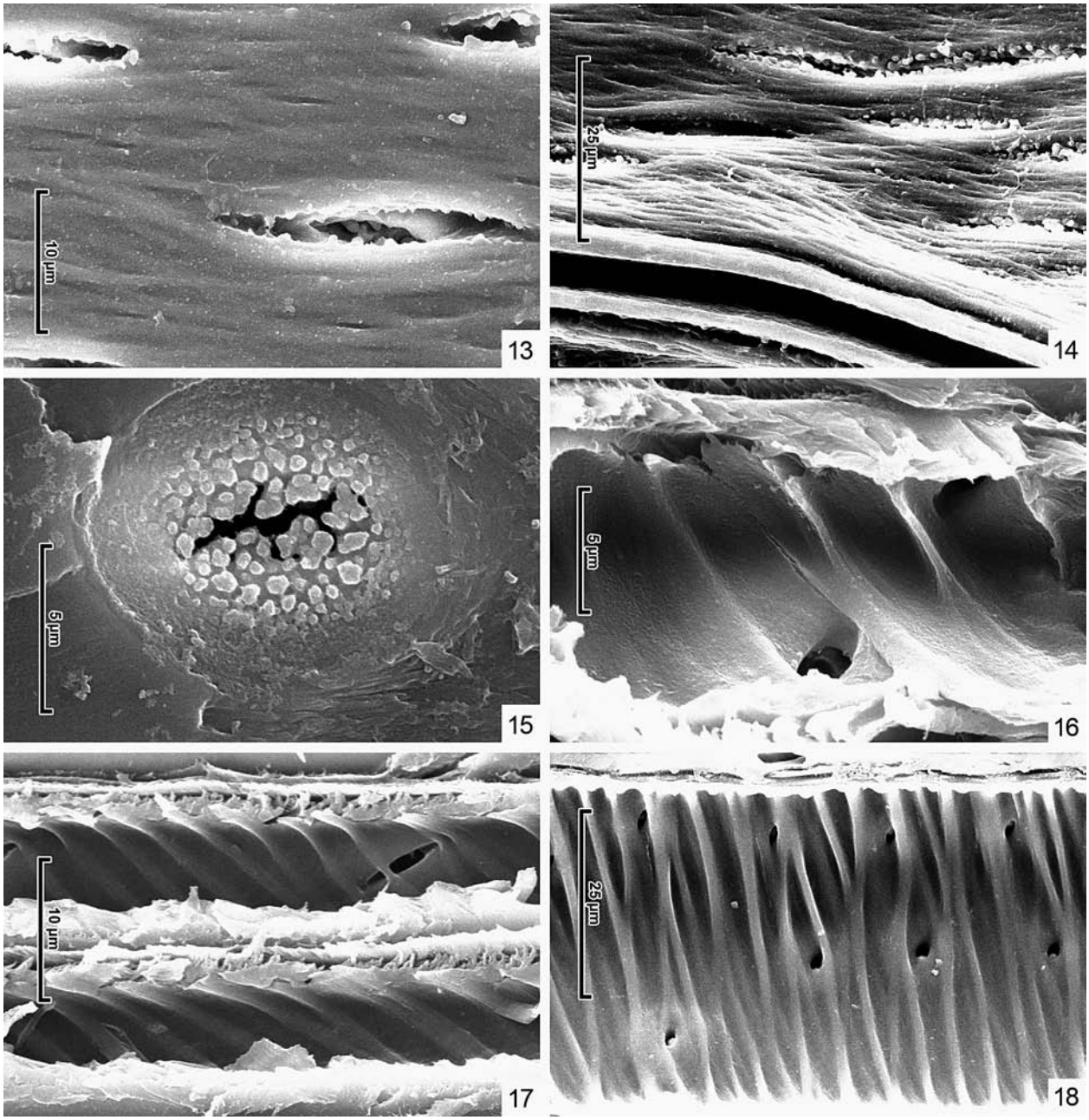

Fig. 13–18. SEM micrographs of forms of wall relief on tracheary elements of *Gnetum* and *Ephedra*.—13–14. *Gnetum cuspidatum*, views of vessel inner surface.—13. Vestured pit apertures, with fine striation on wall surface.—14. Portion of wall near the perforation plate (parallel crescents, below); numerous fine striations are present on wall surface, vesturing extends from pit aperture onto the wall surface.—15–16. *Gnetum africanum*.—15. Vestured pit, seen from outer wall of vessel.—16. Helical thickenings on inner surface of vessel element tip.—17–18. *Ephedra nevadensis*.—17. Helical thickenings on surfaces of portions of two adjacent tracheids.—18. Helical thickenings on inner surface of portion of vessel.

intermediate condition, in which the meshwork is dense, although obviously composed of threads. One can also find pits in which the margo threads are relatively few (Fig. 5). In some pits, the margo threads are virtually invisible. The threads in these pits are essentially fused with the pit border (Fig. 6).

Variation in the porousness of the margo seems to occur randomly. The appearances of Fig. 3–4 are less common. Entirely non-porous margos were figured for *E. equisetina* Bunge earlier (Carlquist 1992: Fig. 20). We have a stereotyped vision of margo porousness, but it does vary considerably among the conifers studied with SEM by Meylan and Butterfield (1978).

The degree of fusion of margo threads with the pit border surface (compare Fig. 1, 2 with Fig. 5, 6) is related to the sectioning process. If less of the pit border of the proximal cell is removed by sectioning (Fig. 2), the pit membranes do not fuse with the pit border. In the pits of Fig. 5 and 6, the proximal portion of the pit pair has been sectioned away. One can use the word ''aspirated'' to describe pit membrane

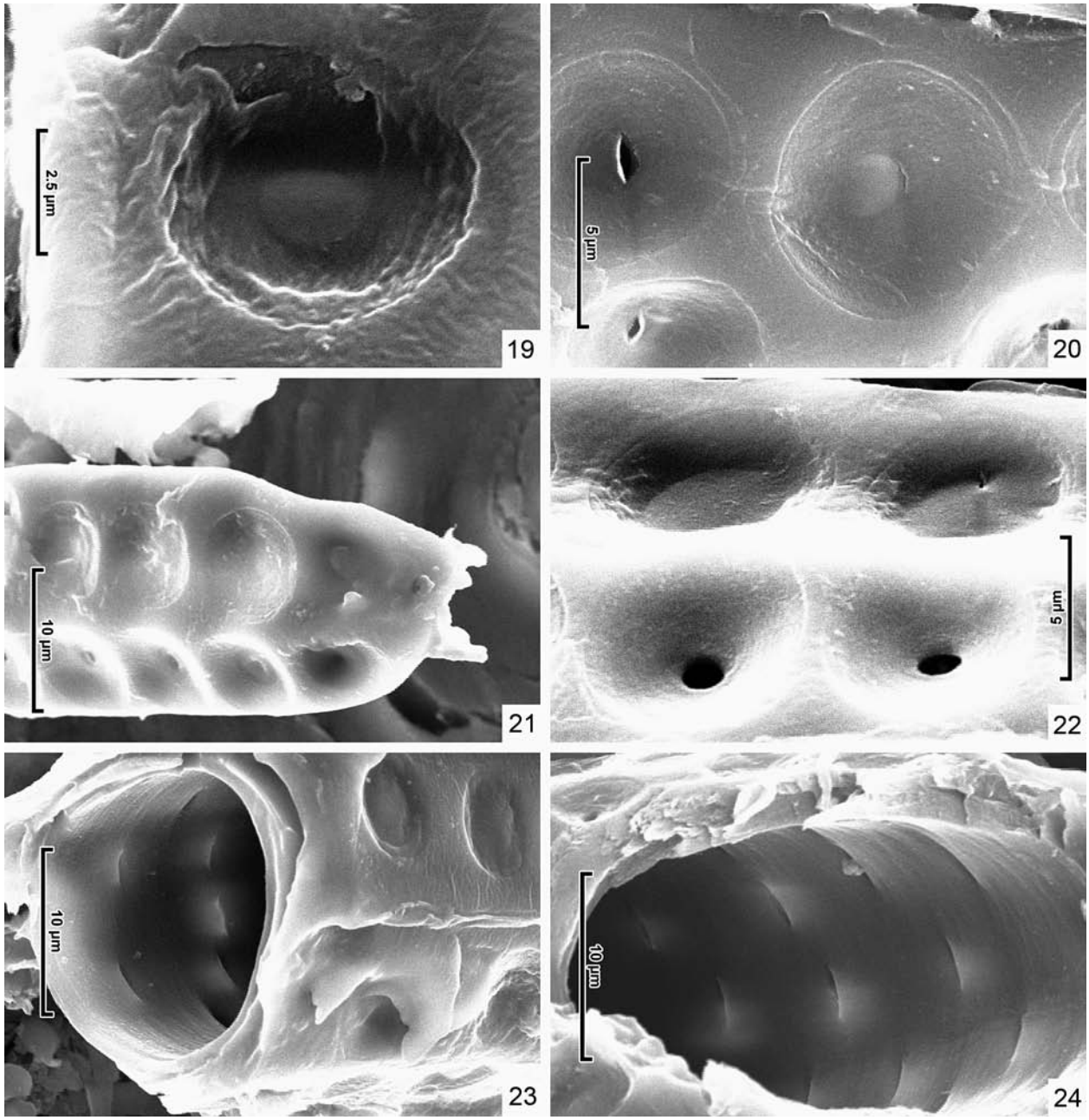

Fig. 19–24. SEM micrographs of tracheary elements of *Welwitschia mirabilis*, from longitudinal or oblique sections of secondary xylem.—19–21. Tracheids, seen from outer surfaces, showing pit membranes sunken into pit borders.—19. Pit membrane with pale central area.—20. Pit membrane at right with pale central area; other pit membranes, at left, do not show such differentiation.—21. Tracheid tip. No differentiation into torus-margo areas is evident except for the pit at upper right near tip.—22–24. Portions of vessels.—22. Two pits that retain pit membranes (above), and two in which the pit membranes have been removed by sectioning (below).—23–24. Vessel sections showing both outer and inner surfaces.—23. Vessel portion. Wall appears two-layered. The two pit membranes at upper right seem to show a moderate torus differentiation.—24. Vessel inner surface, to show very narrow slit-like pit apertures and very fine striation of wall surface.

deflection, although aspiration is a term that has usually been applied to pit membrane deflection in the living plant. The apparent merging of the margo threads with the pit border (Fig. 6) suggests an adherence, perhaps the result of hydrogels in the margo attaching the threads to the pit border surface. In Fig. 1, the portions of the margo threads closer to the torus are intact, whereas portions of the margo threads farther away from the torus have fused with the pit border, indicating partial ''aspiration.'' Pits like those of Fig. 5–6 were more common in my preparations, suggesting that margo displacement is a frequent result of the sectioning process.

Study of light microscope slides of *Ephedra* wood reveals that the torus-margo differentiation of the pit membrane in tracheid pits is universally present. One expects this in tracheid-to-tracheid interfaces, but the fact that it also is present in tracheid-to-vessel interfaces has not been explicitly reported before, and has interesting physiological implications.

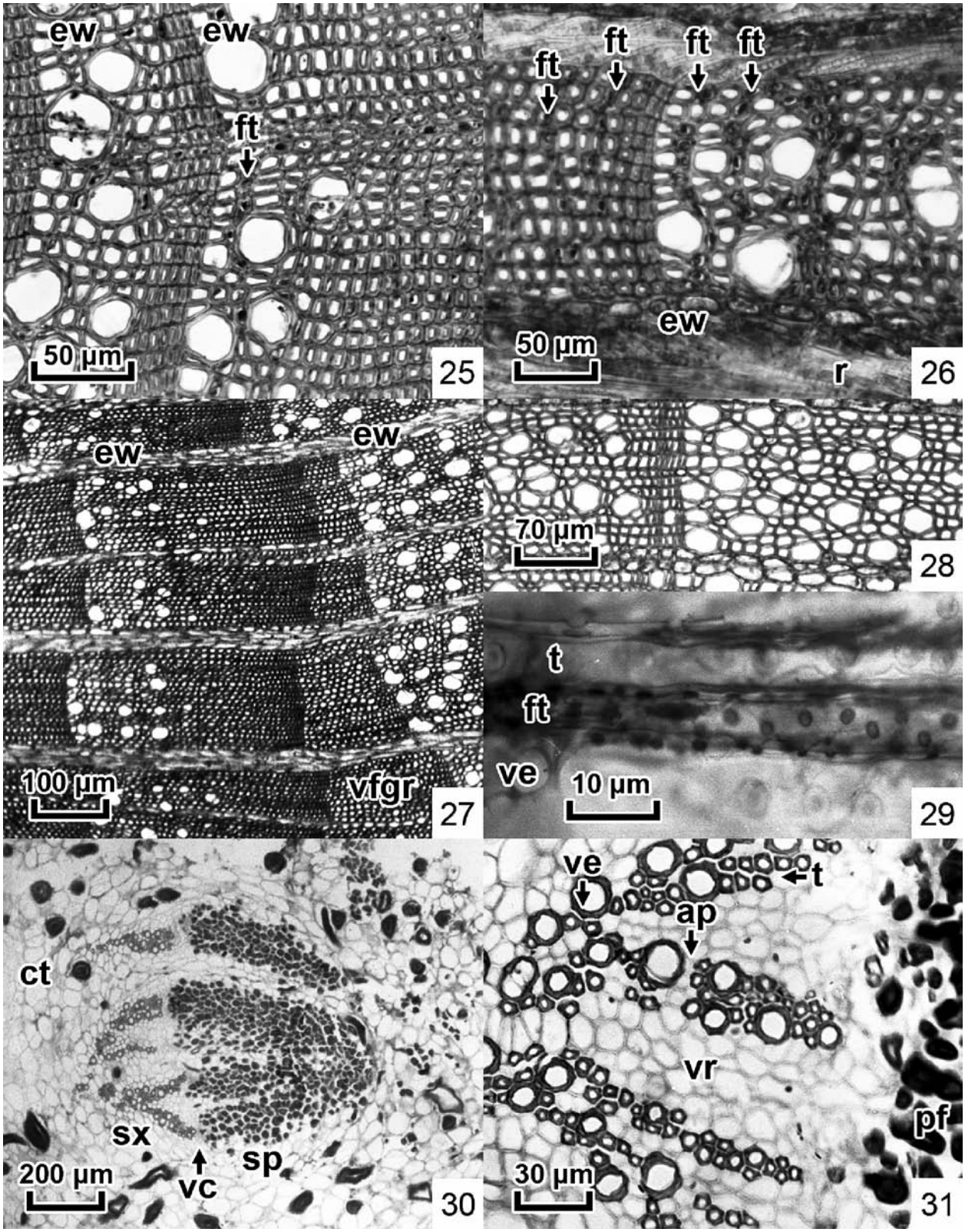

Fig. 25–31. Light photomicrographs of *Ephedra* (25–29) and *Welwitschia* (30–31).—25–26. *Ephedra fasciculata.*—25. Narrow growth ring (left) and portion of a wider growth ring, to show lack of vessels in latewood.—26. Latewood (left) and earlywood (right) of the succeeding growth ring; bands of fiber-tracheids occur in both latewood and earlywood.—27. *Ephedra trifurca.* Several growth rings, from left to right: vessel-free latewood; growth ring with vessels in earlywood but vessel-free latewood; narrow growth ring with no vessels; earlywood of a growth ring.—28–29. *Ephedra pedunculata.* Latewood of one growth ring (left), earlywood of the following ring (right), showing that in this lianoid species, there is minimal difference between latewood and earlywood.—29. Portions of radial section to show, from top to bottom, a tracheid, a

Gnetum.—The pit shown in Fig. 7 represents a typical condition for the tracheids of *G. cuspidatum* stems. Slender and delicate margo threads are evident. These threads are so fragile that at best only half of them survive the sectioning process. As with *Ephedra*, the sectioning process results in pit aspiration frequently, so that peripheral portions of the margo become attached to (and seemingly physically merge with, where imaging is concerned) the pit border (Fig. 8). Some margos in *G. cuspidatum* tracheids are perforated by minute holes, so that a threadlike structure of the margo is not evident (Fig. 9). Tori are visible from the inner surfaces of tracheids (Fig. 10). Such margos are actually quite common in conifers as in the SEM photos by Meylan and Butterfield (1978) for *Dacrydium* Lamb. and *Podocarpus* L'Hér. ex Pers.

Minimally porous margos have been figured for *G. leyboldii* Tul. (Carlquist 1996*b*). Torus-margo differentiation of tracheid pit membranes is also readily seen in light microscope study of *Gnetum* woods (Carlquist 1996*b*: Fig. 4, 5). Torus-margo pit membrane structure in *Gnetum* characterizes not just tracheid-to-tracheid pits, but tracheid-to-vessel pits as well.

Welwitschia.—When viewed with SEM, pit membranes of tracheid and vessel pits sometimes exhibit a paler central circular area suggestive of a torus (Fig. 19–23). Not all bordered pits on tracheary elements of *Welwitschia* possess such a torus-like area (torus-like differentiation is seen in only one of the pits of the tracheid in Fig. 21). No threadlike structure is evident in the margos of *Welwitschia* tracheary element pit membranes. Although some pit membranes are clearly deflected in my preparations (Fig. 22, above) the pit aperture adjacent to the pit membrane is circular (Fig. 22, below), as one would expect in a coniferous tracheid pit. Observations of light microscope preparations of *Welwitschia* tracheary elements have figured slight pit membrane thickenings suggestive of minimal torus-margo differentiation (Bierhorst 1960; Martens 1971).

Vestures

Gnetum is the only genus of Gnetales in which vestured pits have been demonstrated. Minute warts, which could be called vesturing, are present on the inner surface of the pit border in *Libocedrus plumosa* (D.Don) Sargent and *Dacrydium colensoi* Hook. (Meylan and Butterfield 1978) and various Cupressaceae (Pittermann et al. 2010). Vestured pits in *Gnetum* are mostly limited to vessels (Fig. 11–14). The inner surfaces of *Gnetum* tracheids lack vesturing on pits (Fig. 10), but a few vestures have been reported in pits of some tracheids of *G. gnemon* (Carlquist 1994). Vestured pits are illustrated here as seen from the inner surfaces of *Gnetum* vessels (Fig. 11, 13–14), the outer surfaces of *G. cuspidatum* vessels (Fig. 12), the inner surfaces of *G. cuspidatum* vessels (Fig. 13), and the outer surfaces of *G. africanum* vessels (Fig. 15). Vesturing is associated with elliptical pit apertures rather than circular ones, as seen from the inner surfaces of vessels (Fig. 11–14). The non-vestured pits of *G. cuspidatum* illustrated (Fig. 7–10) are tracheid-to-tracheid pits. The torus-margo pit membrane structure can be present both in tracheid-to-tracheid pits and tracheid-to-vessel pits. This is best seen with light microscopy (Fig. 4, 5 in Carlquist 1996*c*).

Helical Thickenings

Ephedra.—Helical thickenings are common in vessels and tracheids of *Ephedra* (Fig. 17–18). About half of the New World species have helical thickenings (Carlquist 1989), but certain Old World species also have them (Carlquist 1992). These thickenings are prominent and can be seen with light microscopy as well as SEM. The thickenings are similar to those reported in ray tracheids and some tracheids (*Pseudotsuga* Carrière) of Pinaceae as well as in tracheids of Cupressaceae (e.g., *Callitris* Vent.) by Greguss (1955).

Gnetum.—Helical thickenings are present in vessels of some species of *Gnetum* (Carlquist 1994, 1996*c*), but they are often fine and run parallel to pit apertures (Fig. 13–14). Helical thickenings can be found in vessel tips of *G. africanum* (Fig. 16). Most vessel surfaces in *Gnetum* are smooth as seen with SEM.

Welwitschia.—The vessels of *Welwitschia* have only inconspicuous forms of helical thickenings (Carlquist and Gowans 1995). Walls of vessels are typically smooth as seen with SEM, and only minor striations are visible (Fig. 23–24). Pit apertures are very narrow and slitlike, and run parallel to striations, if present (Fig. 23–24).

Growth Rings

Ephedra.—Prominent, but diverse growth rings are readily seen in transections of *Ephedra* wood (Fig. 25–28). Vessel-free latewood (Fig. 25–26) is common in *Ephedra*: the species differ only in what portion of the latewood is vessel-free. Only the last several layers of latewood are vessel-free in the liana *E. pedunculata* (Fig. 28), whereas the latewood is entirely vessel-free in *E. trifurca*, with an occasional growth ring entirely free of vessels (Fig. 27, vfgr). *Ephedra* species in alpine deserts may have wood that is almost vessel-free (Carlquist 1988; Motomura et al. 2007). The most common condition in the genus is the formation of earlywood vessels that are relatively narrow (compared with vessels of angiosperms) at first, then even narrower in the transition to vessel-free latewood (Fig. 25–28). Further details of growth rings in particular *Ephedra* species may be found in Carlquist (1988, 1989, 1992).

Gnetum.—Growth ring activity is minimal in most species of *Gnetum*, a fact exemplified by the lianoid species (Carlquist 1996*b*,*c*; Carlquist and Robinson 1995). Diminution of vessel

←

fiber-tracheid (elliptical nucleus left of center), and vessel.—30–31. *Welwitschia mirabilis*, portions of transection.—30. Lower magnification, to show a prominent cap of phloem fibers and the relatively inconspicuous secondary xylem to the left of that.—31. Secondary xylem and, at extreme right, phloem fibers (ap = axial parenchyma; ct = connective tissue; ew = earlywood; ft = fiber-tracheid(s); pf = phloem fibers; r = ray; sp = secondary phloem; sx = secondary xylem; t = tracheid; vc = vascular cambium (inactive); ve = vessel; vfgr = vessel-free growth ring; vr = vascular ray).

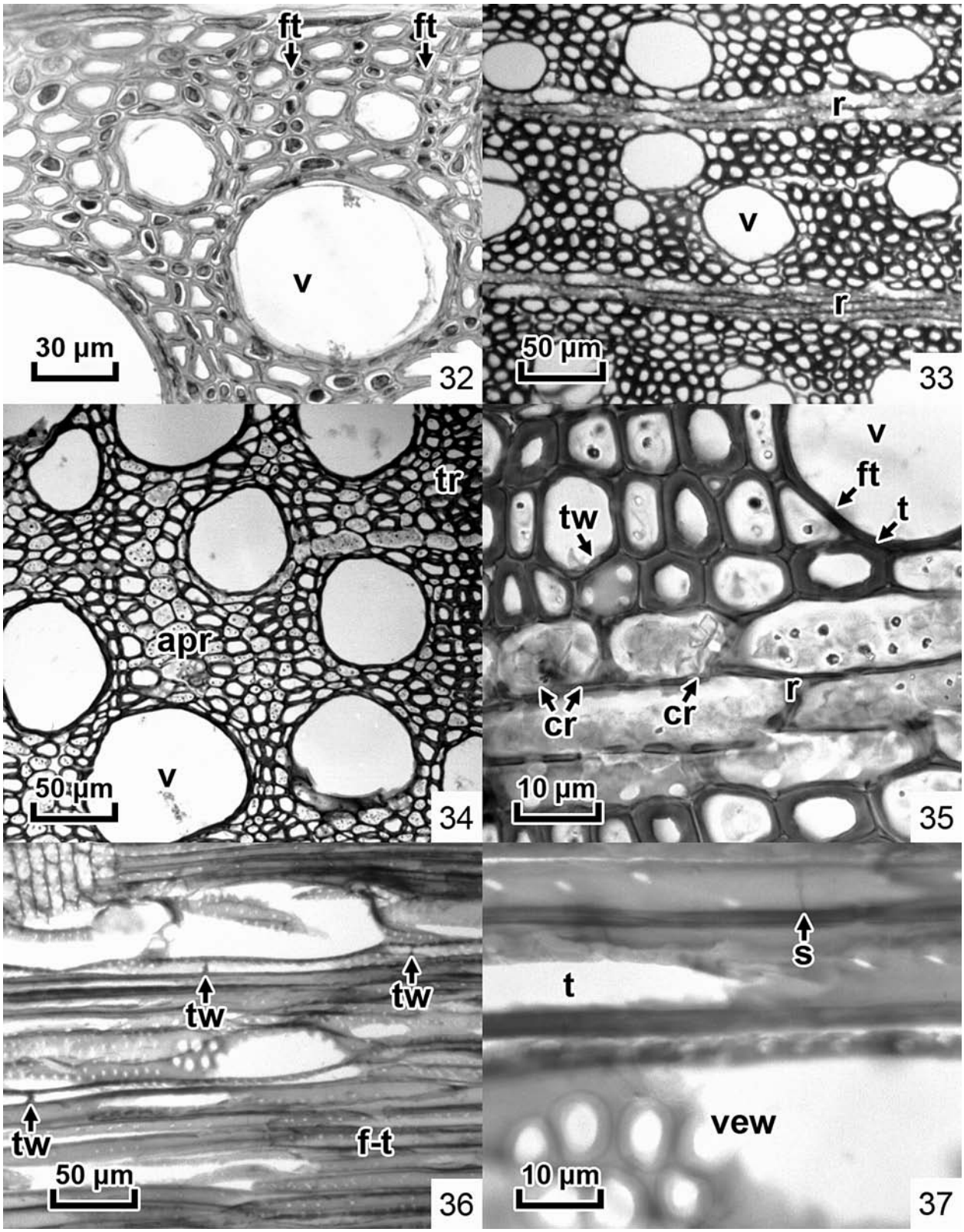

Fig. 32–37. Sections from secondary xylem of *Gnetum africanum* (32) and *G. cuspidatum* (33–37).—32. Portion of transection, to show tendency of fiber-tracheids to occur in bands.—33. Transection of wood from young stem. Vessels are solitary.—34. Transection of wood from root; axial parenchyma is abundant.—35. Transection of stem wood to show various cell types (see key at end of caption) and starch grains (hila of grains mostly appear as black dots).—36–37. Portions of radial sections of wood from young stem.—36. Lower magnification, to show several vessels and some instances of axial parenchyma transverse walls near vessels. 37. Higher magnification, to show details of cell types: septum in fiber-tracheid, top; tracheid, middle; foraminate perforation plate of vessel, bottom. (apr = axial parenchyma-rich region; cr = crystals; ft = fiber-tracheid; r = ray; s = septum; t = tracheid; tw = transverse wall of axial parenchyma strand; v = vessel; vew = vessel element end wall).

diameter indicates latewood formation in *G. gnemon* (Fig. 7 in Carlquist 1994).

Welwitschia.—In *Welwitschia*, there is no evidence of growth ring activity (Fig. 30–31). *Welwitschia* has successive cambia, but these are not formed annually, and in angiosperms that have successive cambia, growth rings may occur at various points within any given vascular increment (Carlquist 2007) rather than annually. Vessel elements and tracheids are always so narrow in *Welwitschia* that all secondary xylem may be considered latewood in character. All wood produced by successive cambia is, by definition, secondary xylem.

Perforation Plate Simplification

Ephedra.—The foraminate perforation plates of *Ephedra* are well known and have been figured on a number of occasions (for SEM photos, see Carlquist 1989, 1992, 1996*a*). The only modifications one can note within *Ephedra* are a reduction in borders of the perforations and increases in the diameter of the perforations. These modifications characterize the species with a scrambling, ascending, or lianoid habit (*E. ciliata* Fisch. & C.A.Mey., *E. kokanica* Regel, *E. pedunculata*: Carlquist 1989, 1992).

Gnetum.—In the lianoid species of *Gnetum*, perforation plates are predominantly simple (Carlquist 1996*b*,*c*; Carlquist and Robinson 1995). The vessels are also typically wider in the lianoid species (although narrower vessels in the liana *G. africanum* can have multiple perforations: Duthie 1912; Maheshwari and Vasil 1961). These two facts are interrelated—perforation plate simplification is often seen in lianoid members of angiosperm clades with scalariform perforation plates, as in Dilleniaceae (Carlquist 2001). The narrow vessels characteristic of young stems of the tree *G. gnemon* frequently have foraminate perforation plates similar to those of *Ephedra* (Fig. 36–37 here; Fig. 13–17 in Carlquist 1994), but simple perforation plates in later-formed wood. Later-formed wood (more recent, peripheral wood, as compared to wood nearer the pith) in mature trees generally has wider vessels, a fact related to trees tapping deeper soil levels as they grow (Carlquist 2001). Compound perforation plates do offer more resistance to flow than simple ones (Christman and Sperry 2010), a fact that has been implicit in the earliest observations on wood evolution in angiosperms.

Welwitschia.—Simple perforation plates characterize *Welwitschia.* A few end walls of vessel elements bear more than one perforation (Bierhorst 1960; Martens 1971).

Axial Parenchyma

Ephedra.—If one is comparing angiosperm wood to gnetalean wood in terms of cell types that may play a role in conductive processes, axial parenchyma is important. Axial parenchyma (subdivided strands of cells) is very scarce in *Ephedra.*

Gnetum.—In *G. gnemon*, axial parenchyma is common adjacent to vessels in stems (Fig. 33; tw in Fig. 35–36) and more common in roots (apr in Fig. 34; tw in Fig. 35 denotes transverse wall of strand). In the lianoid species of *Gnetum*, patches of axial xylem occur interspersed among tracheids and vessels (e.g., *G. buchholzianum* Engl., Carlquist and Robinson 1995; *G. urens* (Aubl.) Blume, Carlquist 1996*c*).

Welwitschia.—There are occasional axial parenchyma strands scattered among the tracheids and vessels of secondary xylem in *Welwitschia* (ap in Fig. 31). These cells are easily identified because of their position in fascicular xylem and their thin walls.

Fiber-Tracheids

Ephedra.—Fibriform cells that have vestigial borders on pits and are nucleate (Fig. 29) are common in *Ephedra.* Septa are lacking. Fiber-tracheids in *Ephedra* are also readily defined because of relatively thin walls (compared to those of tracheids) and contents that stain darkly in preparations made from liquid-preserved material (ft in Fig. 25, 26, 29). Fiber-tracheids in *Ephedra* tend to occur in tangential bands, but may also be found distributed diffusely. They are common in earlywood (Fig. 25), somewhat less frequent in latewood (Fig. 26).

Gnetum.—Tangential bands of fiber-tracheids occur in *Gnetum*. They may be in tangential bands (Fig. 32), adjacent to vessels (Fig. 33) or diffuse. Fiber-tracheids and axial parenchyma combined can be more abundant than tracheids in some wood portions, such as roots (Fig. 34–35). Fiber-tracheids are often septate one or more times (s in Fig. 37) and, like axial parenchyma, have thinner walls (ft in Fig. 35) than tracheids (t in Fig. 35). Occasionally, cells with both septa, characteristic of fiber-tracheids, and cross-walls thicker than septa, characteristic of axial parenchyma, may be found (*G. cuspidatum*, roots). Fiber-tracheids in *Gnetum* have bordered pits, smaller in diameter than those of tracheids. If preparations are made from liquid-preserved specimens, one can see dark-staining contents (Fig. 32) or starch grains (Fig. 35), noticeable by black centers, which are air pockets that develop when material is dehydrated during microtechnical procedures.

Welwitschia.—Fiber-tracheids are absent in *Welwitschia.* There are no cells intermediate between axial parenchyma and tracheids (Fig. 31).

Vascular Rays

Although vascular rays are not directly related to the hydrosystem, they may play an indirect role in the conductive process. They are multiseriate, rarely uniseriate, in Gnetales (Martens 1971; Carlquist 1996*a*). They usually have secondary walls in *Ephedra* (r in Fig. 26) and *Gnetum* (r in Fig. 35), but are thin-walled in *Welwitschia* (Fig. 30–31). Both nucleated fiber-tracheids and vascular ray tissue are more abundant in Gnetales than in non-gnetalean conifers (cf. Greguss 1955).

COMPARISONS: CONDUCTIVE EFFICIENCY VERSUS SAFETY

Data on conductive characteristics are not available for Gnetales other than *Gnetum* (Feild and Balun 2008). Perhaps lack of physiological studies is related to the facts that the species of Gnetales are of little economic interest, they are not readily available, and they are not easily studied with respect to some important physiological measures. The comparisons below are based on features the physiological capabilities of which are experimentally known in angiosperms and non-gnetalean conifers, as reviewed in a recent paper (Carlquist 2012). They are surveyed here to answer the question: what

visible hydraulic adaptations occur in Gnetales? Do these features match the habit and habitat of the genera and species? Some features, such as vessel length (not to be confused with vessel element length) and resistivity (factors countering flow of water in xylem) of woods cannot be observed without experimental means. Indeed, if this categorizing of wood features inspires physiological experimentation, it will have served its purpose. However, we have at present general understandings of which anatomical features increase or decrease flow resistance (Ellerby and Ennos 1998) or enhance surface wettability in conductive cells (Kohonen and Helland 2009). We have working hypotheses of how vessels refill with water after cavitation, which species avoid cavitation, and which species have vessels that embolize daily and refill nocturnally (Holbrook and Zwieniecki 1999; Vogt 2001; Brodersen et al. 2010). Such findings should be applicable to a variety of plants and thereby to broader insights about how wood evolves (Carlquist 2012). Conductive efficiency is defined here as potential increase in volume flow per unit time.

Ephedra

Conductive efficiency.—The presence of vessels in *Ephedra*, apparently in all species, is a step toward conductive efficiency compared with what is provided by an all-tracheid condition, but to a very limited extent. Vessel abundance and vessel diameter are greater in the scrambling or lianoid species; alpine desert species have virtually no vessels, and the vessels are very little wider than the tracheids. Minor modifications in the foraminate perforation plates in terms of perforation size and perforation border reduction indicate very moderate increases in conductive efficiency in the lianoid or scrambling species. The minute leaves and heavily protected stem surfaces (wax coatings, sunken stomata) accord with very limited adaptations to conductive efficiency. Increase in vessel diameter is related to increase in conductive efficiency in vessel-bearing plants at large (Zimmermann 1983).

Conductive safety.—Wood of *Ephedra* is rich in features known to confer conductive safety, that is, prevention of embolism formation or, at worst, confining of embolisms to a smaller number of conductive cells. Tracheids resist embolism formation better than vessel elements because of their pit membranes, and the torus-margo system insures integrity of the water columns of individual tracheids (Zimmermann 1983; Pittermann et al. 2005). By virtue of their numbers, tracheids offer a maximal redundancy. The operation of *Ephedra* latewood entirely on a vesselless basis is a form of maximal conductive safety. Growth rings permit regulation of number and diameter of vessels. While the lianoid and scrambling species have wider and more numerous vessels than the shrubby species, *Ephedra* as a whole shows a strong bias towards safety—with virtually no vessels in the alpine desert species. Even tracheids are narrower in latewood than in earlywood, as in non-gnetalean conifers. Narrow vessels, characteristic of *Ephedra* as a whole, embolize less readily than wider ones and characterize very dry or desert habitats (Carlquist 1966; Carlquist and Hoekman 1985; Hargrave et al. 1994).

Helical thickenings improve wall wettability and thus tend to preserve water columns and aid in their restoration when embolisms occur (Kohonen and Helland 2005). This phenomenon needs further testing. Helical thickenings occur in 14 of 35 species studied and, correlatively, vessel elements are narrower and shorter (Carlquist 1989, 1992). New World species that have thickenings in vessels also have them in tracheids (Carlquist 1989). Not surprisingly, the thickenings characterize the species from more extreme continental climates (Carlquist 1989, 1992).

Most conifer woods have very little axial parenchyma, but *Ephedra* has cells that are equivalent (nucleated fiber-tracheids) and has them in relative abundance. Few vessels or tracheids are not in contact with the fiber-tracheid system, as visualized three-dimensionally. Holbrook and Zwieniecki (1999) and Brodersen et al. (2010) have made a strong case for axial parenchyma as a living system that can change the ion content of water columns or refill them. This argument can be extended to the fiber-tracheids of *Ephedra*, which often form tangential bands so that the vascular rays become part of this living-cell network. Abundant starch storage in fiber-tracheids and rays of *Ephedra* potentially provides a source of sugars for increasing osmotic pressure in water columns, a process demonstrated for angiosperms by Sauter et al. (1973). The starch storage also permits abundant mobilization of photosynthates to take advantage of short periods of water availability for growth and reproduction.

Gnetum

Conductive efficiency.—The broad leaves and mesic habitats of the various species of *Gnetum* would lead us to expect a vessel system biased in terms of conductive efficiency, and that is true. Vessels are relatively wide, more so in the lianoid species than in *G. gnemon* (Carlquist 1994, 1996*b*,*c*; Carlquist and Robinson 1995), validating the applicability of the Hagen-Poiseuille equation (Zimmermann 1983) for relationship between vessel diameter and conductive efficiency. Perforation plate simplification is prominent in *Gnetum* (Maheshwari and Vasil 1971), in contrast to the minor modifications seen in *Ephedra*. Foraminate perforation plates can be found earlier in ontogeny, chiefly in narrower vessels, suggesting that in young stems the balance favors safety more than efficiency: presence of perforation plates impedes flow (Ellerby and Ennos 1998) but tends to confine air embolisms to a single vessel element (Sperry 1985). In angiosperms, wider vessels are less likely to have scalariform perforation plates than narrower ones (Carlquist 1975, 2001). Compound perforation plates do offer appreciable resistance to flow (Christman and Sperry 2010), a phenomenon implied in the earliest concepts of wood evolution (Carlquist 1975, 2001).

Conductive safety.—All species of *Gnetum* have tracheids with torus-margo pit membrane structure. These features are cited by numerous authors (e.g., Pittermann et al. 2005) as indicative of conductive efficiency in (non-gnetalean) conifers. The presence of the torus-margo configuration permits an embolized tracheid to be sealed off from the collective water columns of the tracheid background, so that the embolism does not spread to other tracheids. More importantly, the torus-margo system occurs not just in tracheid-to-tracheid pits, but also in vessel-to-tracheid pits, so that a vessel can be isolated by pit aspiration from collective water columns of the tracheid background when air enters a vessel. This potentially

makes vessel refilling much easier. Refilling in conifer tracheids has not been observed, suggesting that once aspirated, pit membranes may not spring back into position. This may be related to adherence of the threads by hydrogels to the pit borders, as noted above, or tearing in the margo threads.

Axial parenchyma is relatively abundant in *Gnetum*, along with nucleated fiber-tracheids, which are similar in physiological effect. In angiosperms, such cells may serve for refilling of embolized vessels (Holbrook and Zwieniecki 1999; Brodersen et al. 2010).

Welwitschia

The water economy of *Welwitschia* has only recently become understood. Bornman (1978) propagated the hypothesis that fog condensation at night provides mature plants with enough moisture for survival and growth. He envisioned that stomata, supposedly open at night because of CAM photosynthesis, permit entry of water condensed nightly as dew. However, Eller et al. (1983) and others (see Henschel and Seely 2000) have shown that there is little or no CAM activity in *Welwitschia*, and that the stomata are in fact closed at night. According to these authors, the average *Welwitschia* plant transpires more than one liter of water daily, twice the water content of leaves at dawn. Thus, *Welwitschia* depends on drawing water from deep levels in the washes or wash-margins where it grows, and is like other deep-rooted desert wash shrubs with respect to water economy.

Conductive efficiency.—The presence of vessels in *Welwitschia* counts as a step toward conductive efficiency compared with an all-tracheid system, but the narrowness of vessels suggests that the gain is a very moderate one. Vessels are wide enough to be distinguishable from tracheids in transection. With few exceptions, vessels have simple perforation plates (Bierhorst 1960), but the perforations are more like a single pit than a foraminate perforation plate. The narrowness of the vessels would mitigate against foraminate perforation plates.

Conductive safety.—Leaves of *Welwitschia* have transpiration-lowering devices: stomata in grooves, thick cutinization of leaves (Bornman 1978) are more important than narrowness of vessels in confining transpiration to low levels (Willert et al. 1992). Torus-margo differentiation is minimal in pits of *Welwitschia* vessels and tracheids, and as seen with SEM, deflection of the pit membrane is not as pronounced as it is in *Ephedra* and *Gnetum.* The pit membranes also lack evident pores—and pores in the pit margos of conifers are the most important reason for conductive success of an all-tracheid system in non-gnetalean conifers. *Welwitschia* tracheids are not unlike angiosperm tracheids, the pit membranes of which depend on minute pores (much smaller than those of a margo) and relative stiffness to prevent cavitation. Angiosperms with tracheids as a ground tissue often have maximal conductive safety, but compensate for it by having vessels that are more efficient than conifer tracheids. That seems to be the formula in *Welwitschia*.

One feature difficult to estimate is how much of the conductive system in a *Welwitschia* axis—say one a hundred years old—is active. *Welwitschia* has vascular increments produced by successive cambia (Carlquist and Gowans 1995). Angiosperms with successive cambia produce secondary xylem and phloem not just in the most recent vascular increment, but in earlier-formed ones as well. The production of phloem in older increments is indirect evidence that the xylem in older increments, even those no longer producing secondary xylem, is conductively active (Carlquist 2007). At present, we have no estimate of how much older vascular tissue in a *Welwitschia* plant may be active. The best test—uptake of water containing stains—would be easy to do, but would require sacrificing a mature plant.

Axial parenchyma occurs in the secondary xylem of each vascular increment of *Welwitschia.* Working with angiosperms, Holbrook and Zwieniecki (1999) and Brodersen et al. (2010) showed that axial parenchyma, by diffusing ions into adjacent tracheary elements, can maintain them in a conductively active state as well as repair embolisms. Whether or not this occurs in *Welwitschia* needs to be demonstrated.

Gelatinous walls in phloem fibers and sclereids may be a factor in the water economy of *Welwitschia*. Permanent slides show that a large volume of the hypocotyl and root are devoted to these (e.g., Fig. 30) and that they have a much greater cross-sectional area than xylem. Permanent slides also show prominent shrinkage in the walls of the fibers and sclereids, related to the dehydration that occurs in processing. The large volume of such gelatinous walls suggests that fluctuation in water content of the *Welwitschia* axis might occur, and that short-term storage could be a function of the gelatinous walls. Mammalian herbivores do browse the leaves of *Welwitschia* to a moderate extent (Henschel and Seely 2000), but browsing of the axis (hypocotyl plus root) has not been reported, nor does one see any beetle infestation when one views the plants in the wild (original observation). Thus, the phloem fibers do not appear to deter predation (although the crystal-coated sclereids probably do, judging from their dense coatings of calcium oxalate crystals: Carlquist and Gowans 1995).

CONDUCTIVE CAPABILITIES AND SURVIVORSHIP OF GNETALES

The Questions

Gnetales form a small portion of the world's vegetation compared to non-gnetalean conifers, angiosperms, and even ferns. *Ephedra* is a relatively common component of desert scrub in some areas of eastern Asia, southwestern North America, North Africa, and the Middle East, but it is rarely a dominant genus in any particular locality. *Gnetum* and *Welwitschia* are, viewed in a floristic context, rarities. The question that arises when we consider the relictual nature of Gnetales and the conductive adaptations that they have is: what factor or factors are responsible for the relative lack of success of Gnetales, considering their geological age? What accounts for survival of the three genera, respectively, and what role do conductive features play in the ecological adaptations they exhibit? At first glance, Gnetales seem to combine all of the xylem features of angiosperms and all of those of non-gnetalean conifers. If this is correct, why have they not overtaken angiosperms—or the other conifers?

Pittermann et al. (2005) celebrate the torus-margo pit membrane system as the unique advantage that permitted (non-gnetalean) conifers to compete with angiosperms and survive the explosive evolution of angiosperms in Cretaceous and subsequent times. One might perhaps better argue the

reverse, that angiosperms survived in spite of lacking torus-margo pit membrane structure. Tori have evolved in a few clades of angiosperms as apomorphies (Rabaey et al. 2006, 2008; Jansen et al. 2007), and even in those instances, the pit membranes lack the conspicuously porous margos of conifers.

Wood Histology of Gnetales: Histological Advantages

The only cell type present in angiosperm woods that has not been evolved in gnetalean wood is the libriform fiber, which appears to be homoplasious in numerous clades of angiosperms (based on recent phylogenetic trees, e.g., APG III 2009) and is of mechanical rather than hydraulic significance. However, slight modifications of tracheids or of fiber-tracheids in Gnetales seem entirely equivalent to the mechanical wood features of Gnetales. *Gnetum gnemon* manages true arborescence without libriform fibers, and the earlier angiosperms evidently lacked libriform fibers too (Carlquist 2012). Fibriform cells, by sheathing wide vessels in lianas, may protect the vessels from torsion. This is accomplished in *Gnetum* and some angiosperms (*Aristolochia* L., *Schisandra* Michx.) by tracheids, so there is nothing advantageous about an imperforate tracheary element without pit borders for this—or for any other—function related to conduction.

Vessel grouping is a safety device present in a number of angiosperm woods that have libriform fibers or fiber-tracheids. This device is absent in angiosperms with a ground tissue of tracheids, and demonstrates that once libriform fibers had evolved in a clade, vessel grouping became a safety strategy, but not prior to that cell type shift (Carlquist 1984).

The torus-margo pit membrane system, so well developed in *Ephedra* and *Gnetum*, permits the vessels to be hydraulically isolated from the tracheid ground tissue of secondary xylem should an embolism occur in a vessel. Vessels are not weak points where conductive safety is concerned. The vessels of *Gnetum*, potentially vulnerable because of their diameter, have vestured pits, an excellent device for permitting water to re-enter an embolized vessel or even lessening the chance of embolism occurrence (Kohonen and Helland 2009). The vessels of *Ephedra*, judging from vessels of comparable angiosperms, are relatively unlikely to embolize because their diameter is so narrow. Relationship between vessel diameter (which in turn is related to pit area) and vulnerability to cavitation has been shown by a number of authors (Hargrave et al. 1994; Wheeler et al. 2005; Christman et al. 2009; Lens et al. 2011). The helical thickenings on vessels and tracheids of many species of *Ephedra* also probably function in embolism prevention and reversal, judging from the data for this phenomenon presented by Kohonen and Helland (2009). Most species of *Ephedra* have latewood that lacks vessels and is thus minimally vulnerable. The limited foliar surfaces in *Ephedra* correlate with this histological pattern for surviving drought (or freezing).

Axial parenchyma or functionally equivalent fiber-tracheids have a variety of functions. Axial parenchyma is scarce in non-gnetalean conifers or in vesselless angiosperms in comparison with vessel-bearing angiosperms. This cell type has often been treated by anatomy texts as simply a feature of wood to be described, but its function and distribution in woody vascular plants are not covered. This situation is changing, as wood physiologists see ion and sugar content and starch storage as important features of these cells. Anatomical study of woods has all too often been based on dried specimens, and content of living cells, whether axial parenchyma or ray parenchyma, has therefore been downplayed. The paucity of axial parenchyma in non-gnetalean conifers and vesselless angiosperms may relate to different conductive plans. The role of axial parenchyma in conduction (Sauter et al. 1973; Holbrook and Zwieniecki 1999; Brodersen et al. 2010) is finally being appreciated. The role of starch storage, shown here for *Gnetum gnemon*, is mentioned rarely. The abundance of axial parenchyma in *Gnetales* seems intimately related to presence of vessels and regulation of conduction in vessels. The placement of axial parenchyma or living fiber-tracheids in relation to vessels or tracheids also is excellent circumstantial evidence for this relationship (Carlquist 2012).

Thus, Gnetales have all of the wood histological features—and variations on them—that angiosperms do, with minor exceptions. The wood adaptations of the three genera of Gnetales, respectively, match their environments closely with respect to requirements for conductive efficiency and conductive safety. So why have Gnetales not competed better with angiosperms?

Survivorship Strategies of the Three Genera

In terms of area occupied or number of individuals in the wild, *Ephedra* is the most successful of the three genera. Its associates in southwestern North America include shrubs such as *Ericameria* Nutt. (*Chrysothamnus* Nutt.) and *Artemisia* L., which are similar in habit and longevity. Like them, *Ephedra* branches from the base, a good strategy for producing new growth after winter or summer extremes. *Ephedra* can lose branch tips to a greater extent than it produces new ones in an unfavorable year. *Ephedra* survives fire well, partly by resprouting, but partly because seeds are rather fire-resistant and are often buried by the activity of small mammals (West and Hassan 1985). Wood features of *Ephedra*, qualitative and quantitative, are similar to those of other desert woody species in California (Carlquist and Hoekman 1985). Speciation in *Ephedra* relates to edaphic diversity in desert habitats. For example, in southern California, *Ephedra trifurca* grows in sand dunes of lower desert, *E. funerea* Coville & Morton occurs on high desert volcanics, and *E. viridis* Coville occurs in inland winter-cold pinyon-juniper desert, mostly on sandstones (Munz 1974). Similar specializations related to soil and geology could be cited for other species, although detailed comparative data are relatively few. Likewise, at this time, measurements of hydraulic capabilities in *Ephedra* are relatively few.

Gnetum has vessels that are wider in dimensions than those of *Ephedra.* The lianoid species of *Ephedra* are xeromorphs, and not surprisingly, their vessels (Carlquist 1989, 1992) have dimensions larger than those of desert species (Carlquist and Hoekman 1985). The relatively wide diameter of vessels in *Gnetum* has been shown on a number of occasions, both for the tree *G. gnemon* and the lianoid species (Carlquist 1994, 1996*a*,*b*,*c*; Carlquist and Robinson 1995; Fisher and Ewers 1995). However, the vessel diameters of *Gnetum* are moderate compared with those of rain-forest trees and lianas (Carlquist 1975). Not surprisingly, ecophysiological work by Feild and Balun (2008) shows that *Gnetum* hydraulic characteristics are

not those of sunny-habitat canopy trees and lianas. Rather, they resemble those of understory or regrowth shrubs growing in semi-shady situations. Feild and Balun (2008) record hydraulic differences between *Gnetum* and co-occurring lianas and pioneering angiosperms, but these various species may be exploiting similar habitats in different ways. One could cite coffee (which resembles *Gnetum* in appearance) and its ecological requirements as an analogical angiosperm. *Gnetum* plants are comparable with many tropical rain forest angiosperms in size, amount of storage tissue in the seed, and in rate of seedling development.

Welwitschia is often regarded as morphologically, ecologically, and physiologically unique. While appreciating its distinctions, Henschel and Seely (2000) show that *Welwitschia* is related to its habitat as a desert wash shrub in a number of physiological characteristics, and refute the idea that *Welwitschia* meets its water requirements by absorbing moisture condensed from fog as dew. The broad leaves of *Welwitschia* may seem unsuited to the desert habitat of northern Namibia and adjacent Angola, but *Welwitschia* actually mostly occurs within a relatively cool zone 100 km or less from the coast (Henschel and Seely 2000). This zone corresponds to the penetration inland of persistent fogs. Thus, the broad leaf surfaces of *Welwitschia* may be less subject to heating from insolation than one might suppose. In terms of water economy, *Welwitschia* apparently performs like other desert wash shrubs. The occurrence of washes where *Welwitschia* grows, easily seen from the air, suggests seasonal flow from rocky hills that surround these washes, and perhaps even an underground flow from condensation in crevices on the nearby rocky hills. Certainly, *Welwitschia* has no competitors in terms of deep-rooted shrubs where it grows, and the number of co-occurring angiosperm species is very small (Bornman 1978). The roots of desert wash shrubs are much deeper than those of desert scrub plants (Cannon 1911), and the daily transpirational flux of desert wash plants also is much greater than that of desert shrubs (Rundel and Gibson 1996), providing relevant comparisons to the adaptation of *Welwitschia.* To be sure, no desert wash shrub has broad leaves like the two leaves of a *Welwitschia* plant, but perhaps we could consider these two leaves as equivalent to the collective leaf surface of a desert wash shrub such as *Olneya* A.Gray (Fabaceae). This comparison is less facetious than one might think if one considers that numerous vascular increments in a *Welwitschia* axis, many of them probably functional for many years, are collectively equivalent to the basal stem xylem of an angiospermous desert wash shrub. Certainly the tracheids and vessels of *Welwitschia* are very narrow, and comparable to those of desert shrubs (Carlquist 1966; Carlquist and Hoekman 1985).

Gnetales Assessed: Wood Versus Other Features

As noted in the Introduction, Gnetales may have originated in Permian time, and radiated in the Mesozoic. *Ephedra* and *Welwitschia* are recognizable genera by the Cretaceous, but inferential molecular timing for *Gnetum* places its origin later, in the Eocene. Thus, Gnetales apparently predated angiosperms in their origin and competed with them for much of their history. The success of *Welwitschia* and *Ephedra* in dry environments can be keyed to the unsaturated nature of the ecological niches they occupy. Extreme environments are always less saturated than mesic environments because extreme heat, cold, and drought are lethal, whereas constantly mesic conditions are not. This point is easily substantiated by comparing species numbers to latitude, although there is lack of consensus on that correlation, more from zoologists than botanists. If *Ephedra* and *Welwitschia* entered dry habitats early, they had a better chance to succeed against early angiosperms, which appear to have been most abundant in mesic sites (Carlquist 2009, 2012). Recent radiation of angiosperm succulents in desert habitats has been demonstrated by Arakaki et al. (2011).

One can take the position, then, that vegetative adaptations to environments high in stress from extremes of cold, heat, and drought may account for survival of *Ephedra* and *Welwitschia. Gnetum* might have survived merely by shifts to ecological niches within the wet forest habitats to which *Gnetum* as a whole is adapted. The number of successful angiosperm trees and lianas where *Gnetum* occurs is large, so by paralleling foliar and xylary characteristics of such angiosperms, by having reasonably good short-distance dispersal, and by its ability to grow in localities that are shady or with patchy sunlight, *Gnetum* competes just as well as any number of angiosperm species. Although survival in a species-rich wet forest locality might seem more difficult than survival in a high-stress environment, it may require only minor niche-occupancy superiority.

In fact, when we generalize that all but two of the 40 species of *Gnetum* are lianoid, we mislead by use of a single term to cover a variety of habits. *Gnetum cuspidatum* begins as a leaning shrub; it never twines, but is essentially an understory shrub that succeeds in attaining canopy status relatively soon. It produces strobili on cauliflorous shoots near ground level once the leafy crown has reached sufficiently sunlit places (original observations). The cauliflory of the strobili is related to an unusual pollination mechanism (Kato et al. 1995). *Gnetum africanum*, on the other hand, has small thin leaves and twining stems, and grows as an understory woody vine that produces strobili on branch tips (Mike Fay, pers. comm.). *Gnetum schwackeanum* Taub. ex Markgr. grows along river margins, where it cascades over rivers from riparian trees that support it, producing strobili on these well-illuminated branch tips (Dennis Stevenson, pers. comm.). *Gnetum gnemon* is one of only two tree species (the other, *G. costatum* K.Sch., is limited to small areas of New Guinea). I have seen *G. gnemon* reproducing well in regrowth forest on the University of Malaysia campus, Kuala Lumpur; this accords well with the ecological observations of Feild and Balun (2008). To call the various species of *Gnetum* opportunistic might seem an exaggeration, but they are certainly competitive in tropical environments with a wide range of niches.

Rapid reproduction, rather than any advantage of wood anatomy or foliar apparatus, seems to explain why Gnetales have not competed well with angiosperms. Vascular plants, especially angiosperms, seem capable of rapid evolutionary change to conducting systems in order to adapt to shifts in habitat preferences (Carlquist 2012). Even changes with habitat in the torus-margo system have been observed (Hacke and Jansen 2009; Schoonmaker et al. 2010) in non-gnetalean conifers. The necessity to produce a massive female gametophyte prior to fertilization and subsequent embryo formation prolongs embryo formation and is not resource-efficient

compared to angiosperms, in which embryo formation and endosperm are simultaneously developed (Martens 1971). A second (and related) aspect of the slow life cycle characteristics of Gnetales is their requirement for a prolonged period of vegetative growth compared with angiosperms in comparable ecological sites. I know of no species of Gnetales that can flower the first year (or second) after germination. The requirement for greater photosynthate input in order to produce the relatively large seeds of the three gnetalean genera seems clear. In the case of *Ephedra*, the limited photosynthetic surfaces, so essential for resistance to drought and heat, have the simultaneous disadvantage of minimal photosynthate output. If one looks at *Ephedra* in the southwestern United States, one sees such competitors as shrubby species of *Ericameria* (*Chrysothamnus*) and *Artemisia* (both of Asteraceae). These can flower with reasonable abundance during their second year after germination, sometimes with some flowering the first year. Both genera have single-seeded dry fruits that have storage in cotyledons, an advantage for rapid germination. Both recover well after fire, whereas the relatively high percentage of kill of *Ephedra* plants by fire means that restoration of the population from seeds is a requisite. Thus, slow pace of recovery from fire is another feature of slow life-cycling in *Ephedra*.

The earliest angiosperms were probably less woody, but to whatever degree they had woodiness, they were able to shift into both woodier and less woody habits rapidly: they had the advantage of prolonging juvenilism or shortening it (Carlquist 2009). No coniferous species has prolonged production of juvenilistic wood. Thus, no conifer was able to shift rapidly into newly opened habitats compared with angiosperm competitors. The fact that Gnetales have all of the wood anatomical advantages of angiosperms shows that we must look to reproductive efficiency and to ability to shift into new vegetative habits (and thereby into new habitats). The advantages of conifers can be categorized in terms of long-term survivorship. Early angiosperms were probably not as opportunistic as their successors (Carlquist 2012), but they did still have a sufficient edge to outpace Gnetales in all but the most extreme habitats. Wood anatomical features that relate to hydraulics can be demonstrated to shift rapidly in evolutionary terms when one compares them to phylogenetic trees based on molecular information (Carlquist 2012), as demonstrated by wood of lianoid members of predominantly shrubby clades, to cite just one series of examples. The fact that angiosperms have outpaced gymnosperms should be attributed primarily to the inability of gymnosperms to abbreviate their life cycle features: too many changes would be involved. Under this interpretation, gymnosperms have mostly been unable to invade sites with highly seasonal and hydraulically challenging ecology not because of wood limitations, but because of the lack of flexibility that life-cycle considerations impose on them. In Gnetales, as well as in angiosperms, evolution with regard to hydraulically significant features can be considered mostly a matter of shifts in the trade-offs between conductive safety and conductive efficiency.

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